

JOURNAL OF ANIMAL SCIENCE

The Premier Journal and Leading Source of New Knowledge and Perspective in Animal Science

Survival analysis of lamb mortality in a terminal sire composite population

B. R. Southey, S. L. Rodriguez-Zas and K. A. Leymaster

J Anim Sci 2001. 79:2298-2306.

The online version of this article, along with updated information and services, is located on the World Wide Web at:

<http://jas.fass.org>



American Society of Animal Science

www.asas.org

Survival analysis of lamb mortality in a terminal sire composite population¹

B. R. Southey^{*2}, S. L. Rodriguez-Zas^{*}, and K. A. Leymaster[†]

^{*}Department of Animal Science, University of Illinois, Urbana 61801
and [†]USDA, ARS, U.S. Meat Animal Research Center, Clay Center, NE 68933-0166

ABSTRACT: Records of mortality during the first year of life of 8,642 lambs from a composite population at the U.S. Meat Animal Research Center were studied using survival and logistic analyses. The traditional logistic approach analyzes the binary response of whether or not a lamb survived until a particular time point, thus disregarding information on the actual age at death. Survival analysis offers an alternative way to study mortality, wherein the response variable studied is the precise age at death while accounting for possible record censoring. Lamb mortality was studied across five periods based on management practices: birth to weaning, birth to 120 d of age, birth to 365 d of age, weaning to 365 d of age, and 120 to 365 d of age. Explanatory variables included in the models were sex, type of birth, age of dam, and whether or not a lamb was raised in a nursery. The survival analysis was implemented using Weibull and Cox proportional hazards models with sire as random effect. The logistic approach evaluated sire, animal, and maternal effects

models. Lambs culled during any period were treated as censored in the survival analyses and were assumed alive in the logistic analyses. Similar estimates of the explanatory variables were obtained from the survival and logistic analyses, but the survival analyses had lower standard errors than the logistic analyses, suggesting a slight superiority of the former approach. Heritability estimates were generally consistent across all periods ranging from 0.15 to 0.21 in the Weibull model, 0.12 to 0.20 in the Cox model, 0.08 to 0.11 in the logistic sire model, 0.04 to 0.05 in the logistic animal model, and 0.03 to 0.07 in the maternal effects logistic model. Maternal effects were important in the early stages of lamb life, but the maternal heritability was less than 0.07 in all the stages studied with a negative correlation (−0.86 to −0.61) between direct and maternal effects. The estimates of additive genetic variance indicate that the use of survival analysis estimates in breeding schemes could allow for effective selection against mortality, thereby improving sheep productivity, welfare, and profitability.

Key Words: Genetic Models, Heritability, Survival

©2001 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 2001. 79:2298–2306

Introduction

Lamb mortality is a critical component of sheep production systems around the world. Frequently, lamb mortality is analyzed as a binary trait determined by whether or not a lamb survived to a specific age such as weaning. When lamb mortality is commonly ana-

lyzed as either a normally distributed continuous trait or a binary trait, heritability estimates generally range between 0.0 and 0.1 (e.g., Fogarty, 1995; Lopez-Villalobos and Garrick, 1999).

Treating mortality as a binary trait views animal deaths as having occurred during a defined period of time, hence ignoring continuity of the mortality process and the precise time of death or “failure” (Allison, 1997). For example, an animal that dies at 20 d of age would be treated the same as an animal that dies at 200 d of age in a binary analysis of survival from birth to 365 d of age. Survival analysis accounts for the continuity of the mortality and does not restrict the analysis of the data to arbitrary predefined time points. In addition, survival analysis accounts for censored records that occur when the exact time of mortality is unknown because the study concluded before this event can be observed.

Mixed-effects models, commonly used in animal breeding, are referred to as *frailty models* in survival

¹The authors wish to acknowledge V. Ducrocq and J. Sölkner for the use of the Survival Kit; A. R. Gilmour, B. R. Cullis, S. J. Welham, and R. Thompson for the use of their ASREML program; and A. R. Gilmour for assistance in computing the standard errors of heritability. This work was partially supported by the National Center for Supercomputing Applications under grant number MCB990004N and used the computer system SGI Cray Origin2000 at the National Center for Supercomputing Applications, University of Illinois at Urbana-Champaign.

²Correspondence: phone: (217) 244-8751; E-mail: southey@uiuc.edu.

Received November 14, 2000.

Accepted April 23, 2001.

analysis and have been recently reviewed from an animal breeding perspective by Ducrocq (1999), Kachman (1999), and Vukasinovic (1999). Frailty models have been applied to study the length of productive life or longevity in dairy cattle (e.g., Dürr et al., 1999; Vukasinovic et al., 1999) and swine (Yazdi et al., 2000), incidence of mastitis in dairy cattle (Gröhn et al., 1998), and survival in poultry (Ducrocq et al., 2000). These studies have highlighted the advantage of survival analysis over other methods. The objectives of this study are to identify systematic effects influencing lamb mortality and to estimate genetic parameters of lamb mortality using survival and logistic analyses.

Materials and Methods

Description of Population and Management

Data were from a terminal sire composite population (breed composition: 50% Columbia, 25% Hampshire, and 25% Suffolk) at the U.S. Meat Animal Research Center, Clay Center, NE. Leymaster (1991) and Mousa et al. (1999) described the population formation, subsequent management, and breeding practices. Analyzed data were recorded on lambs from the F_3 and advanced generations. Sires were randomly selected within paternal half-sib families from 1983 to 1989. From 1989 onward, half of the sires were randomly selected, and the other half were selected for average daily gain. At least 24 sires were used per year and single-sire mating was performed. Close mating was avoided to minimize the accumulation of inbreeding such that the average inbreeding coefficient was 0.006 for all lambs.

In some years, the breeding season was separated into two periods of 35 d, in which the same rams were used across both breeding periods and ewes were assigned to either the first or second period. Ewes were kept on pasture during gestation and supplemental feeding was used to meet nutritional requirements. Lambing occurred in drylot in a pole-shed facility and ram lambs were not castrated. Lambs whose dams were deemed unable to provide sufficient milk production to sustain lamb survival were artificially reared in a nursery. Lambs were offered ad libitum a total-mixed, preweaning, pelleted diet (2.90 Mcal ME per kilogram DM with 17.5% CP) by 14 d of age. Lambs were weaned at about 7 wk of age and managed under feedlot conditions with access to a pole-shed facility. Lambs were switched to a total-mixed growing diet (2.96 Mcal ME per kilogram DM with 14.5% CP) at approximately 10 wk of age. Lambs remained in drylot until about 20 wk of age when replacement ewes were turned out to pasture with access to supplemental feed. After approximately 20 wk of age, surplus lambs were culled from the main flock on a regular basis.

Lamb records were available from 1985 through 1997 with the date and cause of mortality determined by necropsy for lambs that died. Analyses were conducted on five periods to reflect important periods of lamb pro-

Table 1. Summary statistics for number of records (N), mean survival age (days), standard deviation of survival age (SD), and mortality rate for each period

Period	N	Days ^a	SD	Mortality, %
Birth to weaning	8,642	44	15	15.2
Birth to 120 d of age	8,642	102	40	18.8
Birth to 365 d of age	8,642	222	130	21.6
Weaning to 365 d of age	7,331	210	102	7.6
120 d to 365 d of age	7,020	148	96	3.5

^aMeasured from the start of the period.

duction; mortality from birth to weaning, mortality from birth to 120 d of age, mortality from birth to 365 d of age, mortality from weaning to 365 d of age, and mortality from 120 to 365 d of age. The data analyzed consisted of 8,642 lambs from 299 sires and 2,475 dams, with the number of records, average age, and percentage of mortality for each period provided in Table 1. Of the lambs culled before 365 d of age, 52 were culled before 120 d of age and 3,447 were culled with an average age at culling of 184 d of age.

Statistical Methods

In survival analysis, survival is commonly characterized by a hazard function that represents the instantaneous death rate for an individual surviving to a particular time point (Allison, 1997). The hazard function for individual i at time t , $h_i(t)$, can be described using a linear fixed-effects proportional hazards model with k explanatory variables (x_{i1}, \dots, x_{ik}):

$$\ln[h_i(t)] = \ln[h_0(t)] (\beta_1 x_{i1} + \dots + \beta_k x_{ik}) \quad [1]$$

where $h_0(t)$ denotes an unspecified baseline hazard function and β_1, \dots, β_k are the regression coefficients associated with the k explanatory variables. The baseline hazard function is an arbitrary function common to all observations. The hazard ratio, $h(t)/h_0(t)$, provides an estimate of the risk per unit change in the explanatory variables relative to the baseline hazard function (Collet, 1994; Allison, 1997) and associated SE are approximated as described by Collet (1994).

The Cox proportional hazard and the Weibull models are the most commonly used approaches to model the hazard function (Collet, 1994; Allison, 1997). In the Cox proportional hazards model, the baseline hazard function is unspecified and no assumptions regarding the particular form of this function are required. Alternatively, the natural logarithm of the baseline hazard function can be modeled as $\ln(t)/(\rho - 1)$, implying that the time of event follows a Weibull distribution with Weibull scale parameter ρ (Collet, 1994; Allison, 1997).

Data Analysis

The Cox and Weibull frailty sire models were fitted using the Survival Kit (Ducrocq and Sölkner, 1994,

1998; Sölkner and Ducrocq, 1999). The explanatory variables were sex (two levels; male and female), type of birth (three levels; single, twin, and multiple), contemporary group (18 levels), age of dam (four levels; 1, 2, 3, and 4+ yr of age), and whether or not a lamb was raised in a nursery. Contemporary group was defined as the year of lambing and one of two 35-d breeding periods within year when relevant. The random effect of sire was assumed to have a multinormal distribution, and estimates of location and dispersion parameters were obtained using an empirical Bayesian approach assuming uniform flat improper priors. Estimates of the variance component (mean and mode) were obtained from a Laplacian approximation of the corresponding marginal posterior distribution (Ducrocq and Casella, 1996). Point estimates of fixed and random effects and of ρ (Weibull scale factor) were obtained from the mode of the joint conditional posterior density (Ducrocq and Casella, 1996). Due to the parameterization of ρ in the Survival Kit, the hazard is either accelerated ($\rho > 1$) by a constant factor, degraded ($\rho < 1$) by a constant factor, or held constant ($\rho = 1$). The fixed effects were tested using the Wald test statistic (Collet, 1994; Allison, 1997).

Lambs that were alive at the end of each period were treated as censored at the end of the period because the period ended before mortality could be observed in these lambs. Culled lambs were treated as censored on the day of removal because these lambs were considered to have left the study before mortality could be observed. For censored lambs, only the age until the age at censoring (either due to the end of the period or culling) was used in Eq. [1] for each period. Consequently, the computation of the hazard function associated with a specific time point will include all lambs that are known to be dead or alive at this time point but will exclude any lamb that was censored before this time point.

Binary traits were determined by whether or not a lamb survived to the end of each period and were analyzed using a logistic sire model fitted in ASREML (Gilmour et al., 2000) with the same explanatory variables as the frailty sire models. Logistic animal models and logistic maternal effects models that included random effects for direct additive, maternal genetic, and covariance between direct and maternal effects were also fitted to these binary traits. The ratio of the probability of mortality to the probability of surviving (the odds ratio) was computed in each period for all explanatory variables to correspond to the survival analysis. In all logistic analyses, culled lambs were treated as alive at the end of the period.

Heritabilities in the survival analyses were calculated using modal posterior variance estimates and formulas of Ducrocq and Casella (1996) and Korsgaard et al. (1999) to correspond to heritabilities calculated from the logistic analyses. Approximate SE for the survival and logistic heritabilities and direct-maternal correlation were calculated using the approach described by

Gilmour et al. (2000). Approximate 95% confidence intervals of sire variances obtained from the normal approximation were used to provide 95% confidence intervals for heritability estimates from the sire models.

Results

The Kaplan-Meier estimated survival function for each period (Figure 1) showed that the hazard decreased with time. Each time point of the estimated survival function represents the probability that a lamb will survive to a given day for each period. For example, the estimated probability for a lamb to survive to 10 d of age was 0.9 and to survive to 50 d of age was 0.85 in the birth to weaning, birth to 120 d of age, and birth to 365 d of age periods. Caution is required in the interpretation of these curves because the explanatory effects were unaccounted for and the few lambs experienced an event during the periods studied. The effect of censoring is evident by the drop after 120 d in the weaning to 365 d of age and birth to 365 d of age periods that was associated with an initial culling of lambs from the flock. The drop in survival at the end of the birth to weaning period should be treated with caution due to the few lambs that were weaned at 60 d of age or older. The Weibull scale parameter estimates for most periods ranged from 0.36 ± 0.01 to 0.80 ± 0.05 , indicating that the hazard of mortality decreased over time in agreement with the trend observed in the Kaplan-Meier estimated survival function (Figure 1).

The estimated hazard ratios of the main explanatory variables for the Weibull and Cox models are presented in Tables 2 and 3, respectively. The logistic analyses showed results similar to those of the survival analysis when expressed as an odds ratio (Table 4). Estimates of the explanatory variables were virtually identical between the sire and animal logistic models (results not shown). In all cases, estimates were very similar between all models for the same period considered. The contemporary group effect was significant ($P < 0.01$) in all periods, indicating the variability of environmental and management factors among years.

The sex of the lamb significantly affected mortality in all periods ($P < 0.001$). In the birth to weaning period, the hazard ratio was 1.23 between male and female lambs, indicating that male lambs have 23% greater hazard of mortality than female lambs (Tables 2 and 3). The hazard of mortality increased slightly over time, particularly in the weaning to 365 d of age and the 120 to 365 d of age periods, although the odd ratios (Table 4) were not as large as the hazard ratios (Tables 2 and 3). This result may be somewhat artificial because SE were noticeably larger in the weaning to 365 d of age and the 120 to 365 d of age periods than in the other periods.

Type of birth had an important effect on the hazard of mortality during the birth to weaning, birth to 120 d of age, and birth to 365 d of age periods ($P < 0.001$); all three birth types were significantly different from

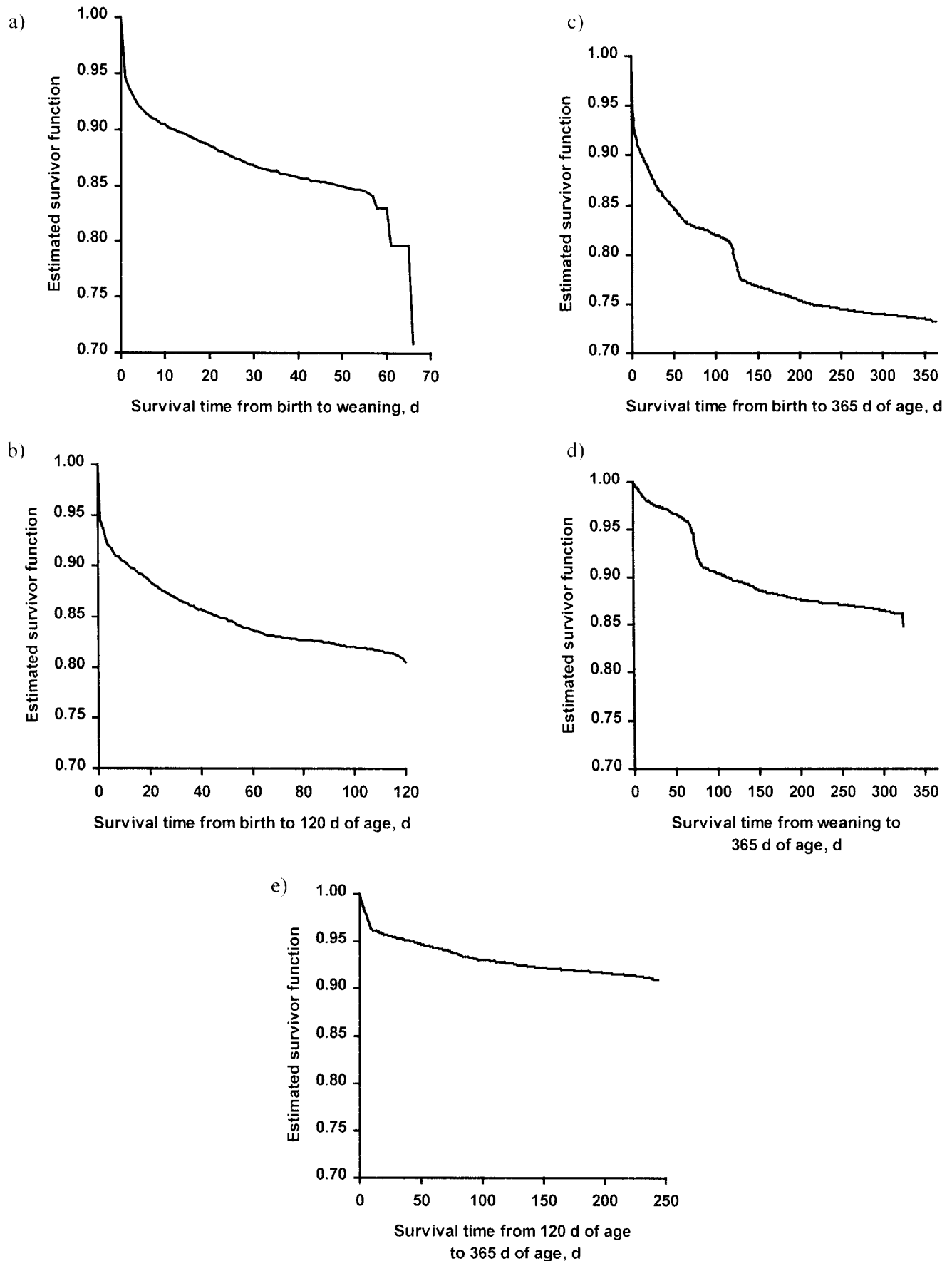


Figure 1. Kaplan-Meier estimated survival functions for a) birth to weaning, b) birth to 120 d of age, c) birth to 365 d of age, d) weaning to 365 d of age, and e) 120 to 365 d of age.

Table 2. Hazard ratios and approximate SE for the explanatory variables for each period under the Weibull sire model

Effect ^a	Period				
	Birth to weaning	Birth to 120 d of age	Birth to 365 d of age	Weaning to 365 d of age	120 to 365 d of age
Lamb sex					
M-F	1.23 ± 0.07	1.22 ± 0.06	1.34 ± 0.06	1.40 ± 0.12	1.59 ± 0.21
Type of birth					
S-M	0.29 ± 0.03	0.37 ± 0.04	0.41 ± 0.04	0.98 ± 0.17	0.86 ± 0.22
T-M	0.47 ± 0.04	0.52 ± 0.04	0.55 ± 0.04	0.82 ± 0.12	0.70 ± 0.15
Age of dam					
1-4	3.01 ± 0.38	2.89 ± 0.33	2.52 ± 0.27	1.60 ± 0.30	0.90 ± 0.26
2-4	1.42 ± 0.16	1.43 ± 0.15	1.35 ± 0.13	1.17 ± 0.20	0.95 ± 0.23
3-4	0.85 ± 0.10	0.92 ± 0.10	0.95 ± 0.09	1.20 ± 0.20	1.12 ± 0.26
Nursery					
N-Y	0.64 ± 0.07	0.47 ± 0.04	0.46 ± 0.04	0.18 ± 0.03	0.54 ± 0.17

^aM-F = effect of male lambs as deviation from female lambs; S-M = effect of single-born lambs as a deviation from multiple-born lambs; T-M = effect of twin-born lambs as a deviation from multiple-born lambs; 1-4 = effect of 1-yr-old ewes as a deviation of 4-yr or older ewes; 2-4 = effect of 2-yr-old ewes as a deviation of 4-yr or older ewes; 3-4 = effect of 3-yr-old ewes as a deviation of 4-yr or older ewes; N-Y = effect of lambs not raised in nursery as a deviation of lamb raised in nursery.

each other (Tables 2 and 3). In these periods, single and twin lambs had 29 to 43% and 47 to 55%, respectively, of the hazard of multiple lambs. It was evident that as the period of consideration lengthened, the relative hazard decreased, which indicates that survival at early stages of life is critical to the overall survival of multiple born lambs than later stages of life. However, type of birth did not have a significant effect on survival during the weaning to 365 d of age and the 120 to 365 d of age periods ($P > 0.05$).

Age of dam (Tables 2 and 3) was important only for lamb mortality for the birth to weaning, birth to 120 d of age, and birth to 365 d of age periods ($P < 0.001$). In these periods, lambs from 1-yr-old ewes had significantly ($P < 0.001$) greater hazard than ewes of all other

ages. Lambs from 2-yr-old ewes had a significantly ($P < 0.001$) greater hazard than 3-yr and the 4-yr and older ewes. No significant difference in hazard rates was observed between 3-yr or older ewes for any of the periods. Age of dam was significant in the weaning to 365 d of age period ($P < 0.05$), with a trend similar to that of the other periods, but was nonsignificant in the 120 to 365 d of age period. Lambs that were raised by their mothers had significantly ($P < 0.001$) lower hazard of mortality (46 to 69%) and lower odds ratio (0.34 to 0.68) than those lambs raised in the nursery for all periods except the 120 to 365 d of age period, for which it was marginally significant ($P < 0.10$).

Variance component and heritability estimates from the sire models (Table 5) showed that the Weibull model

Table 3. Hazard ratios and approximate SE for the explanatory variables for each period under the Cox sire model

Effect ^a	Period				
	Birth to weaning	Birth to 120 d of age	Birth to 365 d of age	Weaning to 365 d of age	120 to 365 d of age
Lamb sex					
M-F	1.23 ± 0.07	1.21 ± 0.06	1.25 ± 0.06	1.30 ± 0.11	1.49 ± 0.20
Type of birth					
S-M	0.31 ± 0.03	0.38 ± 0.04	0.43 ± 0.04	0.99 ± 0.17	0.88 ± 0.22
T-M	0.48 ± 0.04	0.53 ± 0.04	0.55 ± 0.04	0.82 ± 0.12	0.71 ± 0.15
Age of dam					
1-4	2.89 ± 0.37	2.79 ± 0.32	2.42 ± 0.26	1.58 ± 0.30	0.88 ± 0.26
2-4	1.40 ± 0.16	1.42 ± 0.15	1.34 ± 0.13	1.17 ± 0.20	0.95 ± 0.23
3-4	0.85 ± 0.10	0.92 ± 0.10	0.95 ± 0.09	1.20 ± 0.20	1.12 ± 0.26
Nursery					
N-Y	0.69 ± 0.08	0.49 ± 0.04	0.49 ± 0.04	0.19 ± 0.03	0.57 ± 0.18

^aM-F = effect of male lambs as deviation from female lambs; S-M = effect of single-born lambs as a deviation from multiple-born lambs; T-M = effect of twin-born lambs as a deviation from multiple-born lambs; 1-4 = effect of 1-yr-old ewes as a deviation of 4-yr or older ewes; 2-4 = effect of 2-yr-old ewes as a deviation of 4-yr or older ewes; 3-4 = effect of 3-yr-old ewes as a deviation of 4-yr or older ewes; N-Y = effect of lambs not raised in nursery as a deviation of lamb raised in nursery.

Table 4. Odd ratios and approximate SE for the explanatory variables for each period under the logistic sire model

Effect ^a	Period				
	Birth to weaning	Birth to 120 d of age	Birth to 365 d of age	Weaning to 365 d of age	120 to 365 d of age
Lamb sex					
M-F	1.26 ± 0.08	1.24 ± 0.07	1.15 ± 0.06	1.08 ± 0.10	1.35 ± 0.18
Type of birth					
S-M	0.27 ± 0.03	0.34 ± 0.04	0.38 ± 0.04	0.97 ± 0.18	0.87 ± 0.23
T-M	0.45 ± 0.05	0.49 ± 0.05	0.50 ± 0.05	0.80 ± 0.13	0.69 ± 0.16
Age of dam					
1-4	3.21 ± 0.45	3.15 ± 0.41	2.61 ± 0.32	1.52 ± 0.31	0.81 ± 0.24
2-4	1.44 ± 0.18	1.46 ± 0.17	1.37 ± 0.15	1.18 ± 0.21	0.94 ± 0.24
3-4	0.83 ± 0.11	0.91 ± 0.11	0.95 ± 0.10	1.22 ± 0.21	1.12 ± 0.27
Nursery					
N-Y	0.68 ± 0.09	0.34 ± 0.04	0.34 ± 0.04	0.16 ± 0.03	0.60 ± 0.19

^aM-F = effect of male lambs as deviation from female lambs; S-M = effect of single-born lambs as a deviation from multiple-born lambs; T-M = effect of twin-born lambs as a deviation from multiple-born lambs; 1-4 = effect of 1-yr-old ewes as a deviation of 4-yr or older ewes; 2-4 = effect of 2-yr-old ewes as a deviation of 4-yr or older ewes; 3-4 = effect of 3-yr-old ewes as a deviation of 4-yr or older ewes; N-Y = effect of lambs not raised in nursery as a deviation of lamb raised in nursery.

provided the highest estimate of heritability for each period and the logistic sire model the lowest estimate. Heritability estimates ranged from 0.12 to 0.21 for the survival analyses and 0.08 to 0.11 for the logistic analyses. The confidence intervals from all models for the weaning to 365 d of age and the 120 to 365 d of age periods included zero. Although these estimates are not directly comparable due to the different scales and response variables, the largest difference occurred in

birth to weaning period, for which the Weibull estimate was twice the magnitude of the logistic sire estimate.

Under the logistic animal model, estimates of the direct additive variance (Table 6) were less than the corresponding additive variance estimates from the logistic sire model. Consequently, additive heritability estimates were approximately half the magnitude of the logistic sire estimates (Table 5), regardless of whether maternal effects were included in the model or not.

Table 5. Estimates of sire variance (mode, mean, and SE), heritability, and approximate 95% confidence intervals (CI) of the modal estimates for each period from Weibull, Cox, and logistic sire models

Period ^a and model ^b	Sire variance			Heritability		CI bounds	
	Mode	Mean	SE	Est.	SE	Lower	Upper
BW							
Wei	0.090	0.096	0.030	0.207	0.066	0.073	0.332
Cox	0.068	0.074	0.028	0.159	0.063	0.032	0.278
Log	0.086	—	0.031	0.102	0.036	0.058	0.329
BC							
Wei	0.069	0.093	0.026	0.203	0.058	0.086	0.313
Cox	0.069	0.074	0.024	0.161	0.054	0.051	0.265
Log	0.093	—	0.029	0.110	0.033	0.085	0.333
BY							
Wei	0.065	0.069	0.021	0.152	0.048	0.055	0.244
Cox	0.051	0.055	0.020	0.120	0.046	0.028	0.208
Log	0.067	—	0.024	0.079	0.028	0.046	0.259
WY							
Wei	0.082	0.098	0.053	0.190	0.116	0.000	0.404
Cox	0.078	0.094	0.053	0.182	0.117	0.000	0.399
Log	0.077	—	0.052	0.091	0.060	0.000	0.390
CY							
Wei	0.088	0.130	0.090	0.203	0.198	0.000	0.554
Cox	0.086	0.128	0.093	0.200	0.203	0.000	0.561
Log	0.092	—	0.091	0.108	0.105	0.000	0.564

^aBW = birth to weaning; BC = birth to 120 d of age; BY = birth to 365 d of age; WY = weaning to 365 d of age; CY = 120 to 365 d of age.

^bWei = Weibull sire model; Cox = Cox sire model; Log = logistic sire model.

Table 6. Estimates of genetic parameters and heritability for each period obtained using a logistic animal model or a logistic maternal effects model

Parameter	Period			
	Birth to weaning	Birth to 120 d of age	Birth to 365 d of age	Weaning to 365 d of age
Animal effects model				
Animal variance	0.156 ± 0.069	0.156 ± 0.062	0.123 ± 0.054	0.180 ± 0.116
Heritability	0.045 ± 0.019	0.045 ± 0.017	0.036 ± 0.015	0.052 ± 0.032
Maternal effects model				
Direct additive variance (D)	0.115 ± 0.081	0.133 ± 0.076	0.094 ± 0.066	0.225 ± 0.153
Maternal variance (M)	0.244 ± 0.094	0.178 ± 0.080	0.144 ± 0.068	0.021 ± 0.121
Covariance between D and M	-0.114 ± 0.083	-0.098 ± 0.073	-0.071 ± 0.061	-0.059 ± 0.113
Direct heritability	0.034 ± 0.024	0.039 ± 0.022	0.028 ± 0.019	0.066 ± 0.044
Maternal heritability	0.071 ± 0.028	0.052 ± 0.024	0.043 ± 0.020	0.006 ± 0.035
Correlation between D and M	-0.676 ± 0.305	-0.638 ± 0.291	-0.612 ± 0.330	-0.858 ± 1.753

Maternal effects were most important in the birth to weaning period and were nonsignificant in the birth to 365 d of age and the weaning to 365 d of age periods ($P > 0.05$). In all periods, moderately high negative correlations were observed between the direct and maternal effects but were only significant ($P < 0.05$) in the birth to weaning period.

Discussion

The different procedures used to analyze lamb mortality gave very similar results, although, in general, SE for fixed effects from the survival analysis were less than from the logistic analysis. Estimates of the fixed effects were generally very similar between approaches and were relatively consistent with other studies (e.g., Lopez-Villalobos and Garrick, 1999). The similarity of results could have been partly anticipated because, except for the birth to weaning period, the other periods were arbitrarily defined by particular ages. This meant that all surviving lambs at the end of each period had the same age, thus providing similar time scales for the survival and logistic analyses. This may also explain the slightly different results between approaches obtained in the birth to weaning period than in other periods because the survival of lambs within this period uses the actual date of weaning rather than a specific age. A greater difference might have been observed if the end points for each period had not been assigned to a specific age. These end points would need to be predefined to avoid potential bias due to the fact that definition of survival depends on the particular choice of end point.

Literature estimates of the heritability of lamb survival to weaning analyzed as a binary trait typically range from 0.0 to 0.1 (e.g., Fogarty, 1995; Lopez-Villalobos and Garrick, 1999) and were similar to the logistic heritability estimates reported in this study. Gama et al. (1991) and Yapi et al. (1992), however, reported higher heritability estimates from a full-sib analysis (estimates ranged from 0.3 to 0.4) than from a half-sib analysis (estimates ranged from 0.01 to 0.1).

In general, heritability estimates were higher in the logistic sire model than in the logistic animal models, indicating a low to moderate genetic component in lamb mortality. Mayer (1995) also reported similar differences between the animal and sire threshold models. After defining similar sire and animal threshold models, Mayer (1995) attributed the differences to the fact that these models were really not equivalent. The discrepancies between the sire and animal models are expected because, assuming a strictly additive genetic model, these are not linearly equivalent models. The sire variance in the sire models only accounts for one-quarter of the additive genetic variance, whereas the entire additive genetic variance is accounted in the animal model, such that the sire model is overdispersed by definition (Ducrocq and Casella, 1996; Templeman and Gianola, 1996). Further, all the additive genetic relationships are used in the animal model that could lead to an overestimation of the additive genetic variance in the sire model.

The maternal environment is considered to influence lamb survival, but few studies have reported estimates of direct and maternal effects (e.g., Burfening, 1993; Baker, 1998; Lopez-Villalobos and Garrick, 1999). Maternal effects appeared to be important only in the birth to weaning and birth to 120 d of age periods and were not important in the other periods. Hence, the inclusion of the maternal effects in the logistic animal models had a minor influence on the estimated direct additive genetic variance and associated heritability. Gama et al. (1991) and Yapi et al. (1992) considered maternal effects to be a possible explanation of the higher heritability estimates of mortality from a full-sib analysis than from a half-sib analysis. In the birth to weaning period, maternal heritability estimates were similar to those reported by Burfening (1993) and Lopez-Villalobos and Garrick (1999) but higher than those reported by Baker (1998). The nonsignificant maternal component was also observed by Baker (1998) in the weaning to 365 d of age period. The large negative correlation between direct and maternal effects was higher in mag-

nitude than that reported by Lopez-Villalobos and Garrick (1999).

Heritability estimates showed very similar patterns across periods within each sire model. Ducrocq et al. (2000) cautioned against the use of the heritability estimates obtained in a survival analysis because these represent the situation of no censoring. Dürr et al. (1999) reported results from a survival analysis of herd life in Canadian Holstein cows and noted that survival analysis provided higher heritability estimates than those from a logistic approach. This effect is well known from studies comparing threshold models with models in which the predicator is assumed to be normally distributed (Templeman, 1998). The dichotomization of time of mortality causes a loss of information in the logistic analysis that does not occur in the survival analysis. Thus, fewer differences will be observed between animals or sire progeny groups in the logistic analysis than in a survival analysis, resulting in apparently smaller genetic differences than when actual time of mortality is considered. As a consequence, greater estimates of heritability and more effective selection are expected by using a survival analysis than a logistic analysis.

A comparison between the Weibull and Cox survival models is hindered by the different inference made in the approaches. The Weibull model has been preferentially used in animal breeding applications over the Cox model mostly due to lower computational demands (Sölkner and Ducrocq, 1999). The Cox model is widely used in other areas due to the less parametric nature (e.g., Allison, 1997). Within each period, sire breeding values from the Cox and Weibull analyses were very highly correlated (0.99), indicating the same ranking of sires. Ducrocq et al. (2000) also reported very high correlations between breeding values calculated from Cox and Weibull methods for the same trait. This is not unexpected because the same prior for sire variance is used in both approaches. Among the birth to weaning, birth to 120 d of age, and birth to 365 d of age periods, the correlations ranged from 0.87 to 0.95 regardless of the approach. The high correlation is expected due to the fact that subsequent periods contain the same information of the previous period. Correlations between sire breeding values in the weaning to 365 d of age and 120 to 365 d of age periods were lower, ranging from 0.05 to 0.67. This is likely to be a function of the censoring in the data because Vukasinovic et al. (1999) showed that rank correlations between sire breeding values for the same trait dramatically decreased once 0.20 or greater of the records were censored. Therefore, correlations between breeding values have limited merit in model comparison.

Insufficient occurrence of events and the high degree of censoring precluded the estimation of additive genetic variance from a survival model using animal as the random effect in this study. This was partly expected since Ducrocq and Casella (1996) have cautioned against the use of this model when the data have insuf-

ficient information in survival analysis. Estimates of additive genetic variance were obtained from the logistic animal models and the sire models for all periods considered. However, the logistic approach in the birth to 365 d of age, weaning to 365 d of age, and 120 to 365 d of age periods is unable to account for the censoring that occurred when lambs were culled. Therefore, this effectively treats these lambs as alive at 365 d of age, thus providing incorrect inference. This is an important advantage of using survival analysis over the logistic analysis in that the time when censoring occurs is taken into account (Allison, 1997).

In the logistic analysis, the procedure to account for the culled lambs depends on the inference required and the population under consideration. In this study, the logistic approach treated the culled lambs as alive at the end of each period considered, which assumes that all the culled lambs would have survived to the end of the experiment. Alternatively, culled lambs could be treated as dead at the time of culling, which is more restrictive and less desirable because that approach pertains to variable factors such as management and selection decisions. Therefore, provided that culling decisions are independent of mortality, it is more appropriate to treat the culled lambs as censored because it reflects the state of knowledge at the time when the culling decision is made.

Implications

This study highlights the advantage of using survival analysis over the logistic analysis in genetic studies of mortality. This advantage occurs because the Weibull and Cox models describe the precise age of mortality, while accounting for censored records. When age of mortality is categorized into two classes at some specific time point (e.g., alive or dead at weaning), there is a loss of information associated with the actual time of mortality. However, survival analysis requires the availability of records on time of mortality. This study has shown that the logistic analysis provides identical conclusions regarding fixed effects but typically lower heritability estimates compared with the survival analysis. The higher heritability estimates from the survival analysis than from the logistic analysis indicate that selection against lamb mortality using the actual age of mortality can result in improved sheep productivity and profitability.

Literature Cited

- Allison, P. D. 1997. Survival analysis using the SAS system. A practical guide. SAS Institute Inc., Cary, NC, USA.
- Baker, R. L. 1998. A review of genetic resistance to gastrointestinal nematode parasites in sheep and goats in the tropics and evidence for resistance in some sheep and goats breeds in sub-humid coastal Kenya. *Anim. Genet. Resources Inform. Bull.* 24:13–30.
- Burfening, P. J. 1993. Direct and maternal genetic effects on lamb survival. *Small Ruminant Res.* 11:267–274.

- Collet, D. 1994. *Modelling Survival Data in Medical Research*. Chapman and Hall, London, UK.
- Ducrocq, V. 1999. Topics that may deserve further attention in survival analysis applied to dairy cattle breeding: Some suggestions. In: *Proc. of the Int. Workshop on EU Concerted Action on the Genetic Improvement of Functional Traits in Cattle (GIFT)—Longevity*. Jouy-en-Josas, France. INTERBULL Bull. No. 21:181–189.
- Ducrocq, V., B. Besbes, and M. Protais. 2000. Genetic improvement of laying hens viability using survival analysis. *Genet. Sel. Evol.* 32:23–40.
- Ducrocq, V., and G. Casella. 1996. A Bayesian analysis of mixed survival models. *Genet. Sel. Evol.* 28:505–529.
- Ducrocq, V., and J. Sölkner. 1994. The survival kit, a FORTRAN package for the analyses of survival data. In: *Proc. 5th World Cong. Genet. Appl. Livest. Prod.*, Gullph, Canada. 22:51–52.
- Ducrocq, V., and J. Sölkner. 1998. The survival kit - V3.0, a package for large analyses of survival data. In: *Proc. 6th World Cong. Genet Appl. Livest. Prod.* Armidal, NSW, Australia. 27:447–448.
- Dürr, J. W., H. G. Monardes, and R. I. Cue. 1999. Genetic analysis of herd life in Quebec Holsteins using Weibull models. *J. Dairy Sci.* 82:2503–2513.
- Fogarty, N. M. 1995. Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction: A review. *Anim. Breed. Abstr.* 63:101–143.
- Gama, L. T., G. E. Dickerson, L. D. Young, and K. A. Leymaster. 1991. Genetic and phenotypic variation in sources of preweaning lamb mortality. *J. Anim. Sci.* 69:2744–2753.
- Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 2000. *ASREML Reference manual* [mimeo]. New South Wales Agriculture, Orange, Australia.
- Gröhn, Y. T., V. Ducrocq, and J. A. Hertl. 1998. Modeling the effect of a disease on culling: An illustration of the use of time-dependent covariates for survival analysis. *J. Dairy Sci.* 80:1755–1766.
- Kachman, S. D. 1999. Applications in survival analysis. *J. Anim. Sci.* 77 (Suppl. 2):147–153.
- Korsgaard, I. R., A. H. Andersen, and J. Jensen. 1999. Discussion of heritability of survival traits. In: *Proc. of the Int. Workshop on EU Concerted Action on the Genetic Improvement of Functional Traits in Cattle (GIFT)—Longevity*. Jouy-en-Josas, France. INTERBULL Bull. No. 21:31–35.
- Leymaster, K. A. 1991. Straightbred comparison of a composite population and the Suffolk breed for performance traits of sheep. *J. Anim. Sci.* 69:993–999.
- Lopez-Villalobos, N., and D. J. Garrick. 1999. Genetic parameter estimates for survival in Romney sheep. *Proc. N. Z. Soc. Anim. Prod.* 59:121–124.
- Mayer, M. 1995. Inequality of maximum a posteriori estimators with equivalent sire and animal models for threshold traits. *Genet. Sel. Evol.* 27:423–435.
- Mousa, E., L. D. Van Vleck, and K. A. Leymaster. 1999. Genetic parameters for growth traits for a composite terminal sire breed of sheep. *J. Anim. Sci.* 77:1659–1665.
- Sölkner, J., and V. Ducrocq. 1999. The Survival Kit: A tool for analysis of survival data. In: *Proc. of the Int. Workshop on EU Concerted Action on the Genetic Improvement of Functional Traits in Cattle (GIFT)—Longevity*. Jouy-en-Josas, France. INTERBULL Bull. No. 21:11–16.
- Templeman, R. J. 1998. Generalized linear mixed models in dairy cattle breeding. *J. Dairy Sci.* 81:1428–1444.
- Templeman, R. J., and D. Gianola. 1996. A mixed effects model for overdispersed count data in animal breeding. *Biometrics* 52:265–279.
- Vukasinovic, N. 1999. Application of survival analysis in breeding for longevity. In: *Proc. of the Int. Workshop on EU Concerted Action on the Genetic Improvement of Functional Traits in Cattle (GIFT)—Longevity*. Jouy-en-Josas, France. INTERBULL Bull. No. 21:3–10.
- Vukasinovic, N., J. Moll, and N. Künzi. 1999. Genetic evaluation for the length of productive life with censored records. *J. Dairy Sci.* 82:2178–2185.
- Yapi, C. V., W. J. Boylan, and R. A. Robinson. 1992. Heritability and repeatability estimates and the correlations of lamb mortality with birth weight and litter size. *World Rev. Anim. Prod.* 27:55–60.
- Yazdi, M. H., L. Rydhmer, E. Ringmar-Cederberg, N. Lundeheim, and K. Johansson. 2000. Genetic study of longevity in Swedish Landrace sows. *Livest. Prod. Sci.* 63:255–264.

Citations

This article has been cited by 5 HighWire-hosted articles:
<http://jas.fass.org#otherarticles>